

Pontoporeia hoyi—a Direct Trophic Link between Spring Diatoms and Fish in Lake Michigan

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ABSTRACT Several lines of evidence suggest that the Lake Michigan benthic amphipod, *Pontoporeia hoyi* (an important fish prey in large, temperate, low-nutrient lakes), may obtain a large portion of its annual energy directly from the spring diatom bloom: 1) Energetic considerations suggest that *P. hoyi* must assimilate a large fraction of energy from incoming organic material, but that summer input rates are not sufficient to support observed annual production of *P. hoyi*. 2) The weight-specific lipid content of *P. hoyi* at some locations in Lake Michigan doubles within a few weeks after the spring diatom bloom. 3) Lipids accumulate in *P. hoyi* primarily as the storage products, triglycerides. 4) *P. hoyi* feeds intermittently and can survive for months without food. 5) The dominant spring diatom in Lake Michigan, *Melosira*, is not significantly cropped by zooplankton and settles rapidly through the water column in the spring and early summer. 6) After the spring diatom bloom, the phytoplankton changes to a dominance of flagellates that are mostly eaten by pelagic zooplankton and therefore largely unavailable to benthic organisms.

The ability of *P. hoyi* to rapidly accumulate and store energy from spring diatom blooms may help explain why this amphipod thrives in many temperate, oligotrophic/mesotrophic lakes. This apparently direct trophic linkage between spring diatoms and *P. hoyi* is energetically important because it involves a minimum of trophic energy loss between primary production and fish.

Pontoporeia hoyi, the dominant benthic invertebrate in the upper Great Lakes, constitutes about 65% of the benthic-invertebrate biomass in southern Lake Michigan (Nalepa et al., 1985). This amphipod is a desirable fish prey that is consumed by various developmental stages of most Great Lakes fish species (Wells, 1980). Despite the importance of *P. hoyi* to fish, pathways between primary producers and *P. hoyi* have not previously been detailed. *P. hoyi* has

generally been considered to be a detritivore that prefers small particles enriched with organic material or bacteria (Marzolf, 1965). Food availability was reported to be the critical factor limiting growth of *Pontoporeia* in Lake Mälaren, Sweden (Wiederholm, 1973; Johnson and Wiederholm, 1989). Studies in the Baltic Sea have linked spring phytoplankton sedimentation with subsequent production of *Pontoporeia* species (Cederwall, 1977), but linkage between sedimented phytoplankton blooms and subsequent *P. hoyi* growth has not been established as definitively in the North American Great Lakes. In this paper, we summarize some of our recent Lake Michigan experiments showing that energy may be transferred quite directly from spring diatoms to *P. hoyi* and suggest that *P. hoyi* exploits seasonal inputs of high-quality food in the Great Lakes.

34.1 Areal Comparisons of Sediment-Trap Inputs to Annual *P. hoyi* Production

Initially, we compare inputs of organic material, estimated by sediment-trap collections, to areal *P. hoyi* metabolic rate processes (biomass-production and excretion rates). Net particulate organic carbon (POC) inputs into the hypolimnion of Lake Michigan were estimated for 1980 (Eadie et al., 1984) from the mass flux and organic carbon content of sediment trap materials collected below the epilimnion during the period of summer stratification. These materials were collected in traps suspended at 35-m depth at four stations (offshore from Grand Haven, Michigan) with total depths ranging from 83 to 102 m (Eadie et al., 1984). Sediment-trap collections made during the period of stratification were thought to provide a better estimate of "freshly produced" organic particles than estimates made during holomixis because they did not contain significant amounts of "old" resuspended particles from the hypolimnion. Using this approach, average inputs of "new" organic carbon at four offshore stations in southern Lake Michigan were estimated to be $63 \pm 36 \text{ mg m}^{-2} \text{ d}^{-1}$ (Eadie et al., 1984), or $23 \text{ g m}^{-2} \text{ y}^{-1}$ if summer rates were extrapolated over the annual cycle.

P. hoyi production in Lake Michigan was calculated from mean areal *P. hoyi* biomass estimates and production/biomass (P/B) ratios reported for the organism (Lubner, 1979; Winnell and White, 1984). Mean areal *P. hoyi* biomass [$2.76 \text{ g AFDW (ash-free dry weight) m}^{-2}$] was determined from a 40-station grid sampled in 1980–1981 (Nalepa et al., 1985) by summing areal-weighted biomass estimates from various regions (Gardner et al., 1985a). Mean areal biomass was multiplied by an annual P/B ratio (about 1.2 for *P. hoyi* in offshore Lake Michigan; Lubner, 1979; Winnell and White, 1984) to calculate the mean productivity of *P. hoyi* in southern Lake Michigan ($3.3 \text{ g AFDW m}^{-2} \text{ y}^{-1}$). Assimilation efficiencies have not been estimated, but based on a growth-efficiency range of 0.3 to 0.6 for *P. hoyi* (Johnson and Brinkhurst, 1971), this calculation suggests that *P. hoyi* must assimilate at least between 5.5 to 11 g

$\text{m}^{-2} \text{y}^{-1}$ of organic detritus (Gardner et al., 1985a). More recent work indicates that Ponar grab samples underestimate actual *P. hoyi* biomass by a factor of 1.5 (Nalepa et al., 1988). With this correction, the calculated minimum requirements of *P. hoyi* would be 8.2 to 16.5 g POM (particulate organic matter) $\text{m}^{-2} \text{y}^{-1}$ (or 4.1 to 8.2 g C $\text{m}^{-2} \text{y}^{-1}$, assuming a carbon to biomass ratio of 0.5). This food requirement equals 18 to 36% of the organic C input as estimated above from summer sediment-trap accumulation rates of offshore material (Eadie et al., 1984). If the summer sediment-trap input rates provide a reasonable estimate of the annual supply of new available material to the benthos, this calculation suggests that a relatively high percentage of freshly settled organic material must be assimilated by *P. hoyi* and other benthic invertebrates (Gardner et al., 1985a). However, nearly complete assimilation of ingested material probably is not a good assumption, particularly if the food quality is low, as may be expected for benthic-detrital material. In addition, if settling rates are slow, a portion of the particles (measured at near-thermocline depth) would probably be eaten or decomposed in the water column before becoming available to the benthic invertebrates. Thus the "observed" level of *P. hoyi* productivity appears higher than expected if estimated summer input rates are assumed to represent maximum available food supply.

Similar comparisons were made by comparing areal *P. hoyi* nitrogen regeneration rates, as measured by ammonium excretion, to areal inputs of particulate organic nitrogen. Seasonal studies of ammonium excretion by *P. hoyi* in southeastern Lake Michigan (Gauvin et al., 1989; Gardner et al., 1987) indicate that ammonium excretion rates of *P. hoyi* range from about 1 to 4 ng atom nitrogen (mg AFDW) $^{-1} \text{h}^{-1}$.^{*} Assuming this range of excretion rates, and an areal *P. hoyi* biomass of 4.1 g AFDW m^{-2} (see above), the mean areal excretion rate for *P. hoyi* would range between 0.5 and 2.0 g N $\text{m}^{-2} \text{y}^{-1}$ as compared to a Kjeldahl nitrogen input rate of 2.3 g N $\text{m}^{-2} \text{y}^{-1}$, as extrapolated from summer sediment-trap data (Eadie et al., 1984). If approximately as much nitrogen is assimilated for growth as is excreted by *P. hoyi* (N growth efficiency = 0.5), the total nitrogen requirement would be 1 to 4 g N $\text{m}^{-2} \text{y}^{-1}$. This calculation indicates that incoming particulate organic nitrogen, as measured in the summer, may not be sufficient to account for nitrogen assimilation by *P. hoyi* and other benthos. An explanation for these apparent inconsistencies between estimated nutritional inputs and *P. hoyi* production and excretion rates is that annual rates of food supply were underestimated by extrapolating summer input rates over the whole season. Recent seasonal sediment-trap studies indicate that the fluxes of "potentially available" nutrient indicators (AFDW, organic nitrogen, total lipids, biogenic silica) peak in the spring (Gardner et al., 1989).

^{*}As would be expected, these rates are much lower than those reported for warm-water pelagic species, e.g., 35–83 ng atom nitrogen (mg dry weight) $^{-1} \text{h}^{-1}$ for *Daphnia* (Lehman, 1980), or for other benthic macroinvertebrates held at relatively high temperatures, e.g., 5–14 ng atom nitrogen (mg AFDW) $^{-1} \text{h}^{-1}$ for chironomids and tubificids held at 22°C (Gardner et al., 1983).

34.2 Biochemical/Physiological Studies of *P. hoyi*

Insights about seasonal trends in the transfer of energy to *P. hoyi* and about the possible role of spring diatoms in this exchange were gained by examining seasonal changes in lipid content (Gardner et al., 1985a), lipid composition (Gardner et al., 1985b), and feeding patterns of *P. hoyi* (Quigley, 1988).

In the early spring, lipids constituted about 20 to 25% of the AFDW of *P. hoyi*, but within a period of weeks, mean lipid content of the animals dramatically increased to 40 to 50% of AFDW (Figure 34.1). This increase in lipid content corresponded in time to expected inputs of diatoms from the spring bloom and suggests a likely direct link between the diatoms and *P. hoyi*, as observed in the Baltic Sea for *P. affinis* (Cederwall, 1977). Similar patterns of lipid accumulation were observed in subsequent years (Gauvin et al., 1989; Landrum, 1988). A more recent comparison of alkane ratios (C-17:C-29) in seasonally collected sediment trap materials indicated that fresh phytoplankton constituted a higher proportion of the trap materials during the period immediately preceding the observed increases in *P. hoyi* lipid content than during other parts of the year (Gardner et al., 1989).

To differentiate the effects of incoming food on lipid content from other season-dependent factors, *P. hoyi*, collected in spring, were divided into two groups and incubated in the laboratory. One group was held for 80 days in filtered lake water whereas the other group was held in lake sediments with no fresh additions of particles. The lipid content of constituent animals was determined over time and compared to that of animals collected in the field over the same interval. The results (Figure 34.2) showed pronounced differences among the three groups. The mean lipid content of animals held in filtered lake water decreased during the incubation period of about 80 days to about 12% of animal dry weight. Lipids in animals held in lake sediments remained relatively constant over the first 40 days of incubation and then decreased relative to dry weight. Thus, in contrast to the lake animals, neither

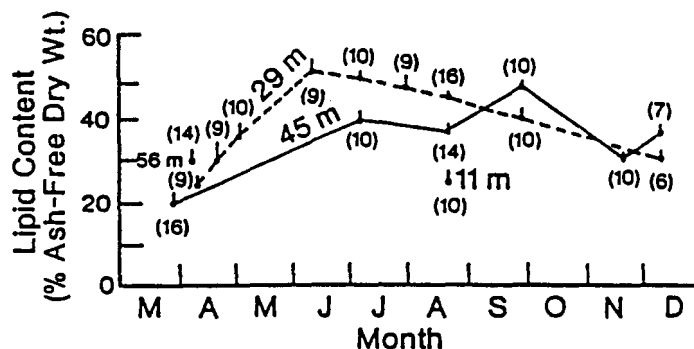


Figure 34.1 Total lipid content, relative to AFDW, in *Pontoporeia hoyi* sampled seasonally from southeastern Lake Michigan in 1984. Range bars = standard errors. Numbers in parentheses represent the number of replicate animals analyzed. (Modified from Gardner et al., 1985a.)

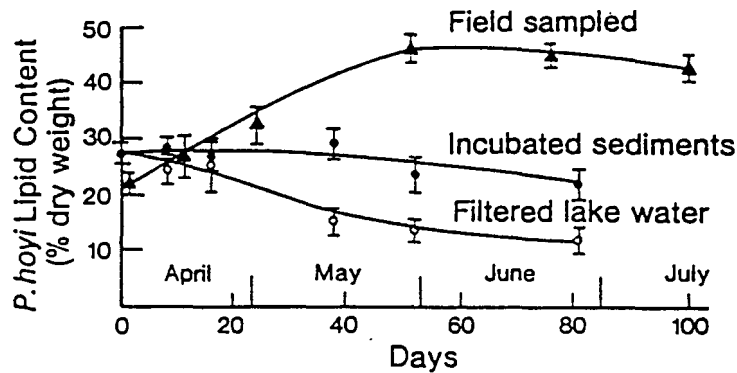


Figure 34.2 Lipid content, relative to dry weight, in *P. hoyi* samples collected directly from Lake Michigan and those incubated in the laboratory in the presence and absence of natural sediments. *P. hoyi* samples analyzed directly after collection were taken from a site directly offshore from Grand Haven, Michigan, at a water depth of 24 m. Incubated animals were collected offshore from South Haven, Michigan at a depth of 56 m in April 1984. Range bars = standard errors.

laboratory group showed a springtime increase in lipid content. Similar results were observed in a subsequent study (Gauvin et al., 1989). Although other factors, such as possible differences in feeding activities between laboratory and field animals, cannot be completely disregarded, *in situ P. hoyi* populations received inputs of sedimenting spring diatoms, while laboratory populations did not. The differences in lipid accumulation among the groups support the hypothesis that *P. hoyi* may accumulate lipids from settling diatoms.

Further insights about the use of lipids for energy storage by *P. hoyi* were gained by examining lipid-class composition. Class analysis of lipids in *P. hoyi* collected from Lake Michigan in August 1984 (Gardner et al., 1985b) indicated that triglycerides are the dominant lipid component in *P. hoyi*. Triglycerides are accumulated by organisms specifically for the purpose of storing energy (Lee, 1975). Although we did not examine lipid compositional changes in the seasonal study, more recent laboratory experiments indicate that triglycerides are the main lipid class reflecting observed changes in total lipids in *P. hoyi* (unpublished data).

Examination of *P. hoyi* gut fullness (Quigley, 1988) indicated that Lake Michigan *P. hoyi* populations intensify their feeding in spring. Highest mean percent gut fullness was 59% in March and declined through the summer to approximately 40%. The incidence of animals with empty and partially filled guts also suggested that *P. hoyi* feed intermittently rather than in the continuous mode commonly noted among amphipods. In general, guts of continuously feeding animals remain constantly full (Moore, 1977; Marchant and Hynes, 1981). *P. hoyi*'s intermittent feeding habits are unusual, but not surprising, given their ability to accumulate and store lipids. In fact, lipid storage may afford *P. hoyi* the option of exploiting high-quality food when it becomes available (i.e., following sedimentation of the spring diatom bloom). At other times, the animals may rely on stored lipids to satisfy normal metabolic energy re-

quirements, while feeding at a reduced rate. *P. hoyi*'s lipid-storage capability may, in part, explain the amphipod's widespread distribution throughout the upper Great Lakes (Cook and Johnson, 1974) and other environments where high-quality food resources are often limited. Further insights into sources of "high-quality" food for *P. hoyi* were gained by seasonal investigations of epilimnetic phytoplankton and settling particles in Lake Michigan.

34.3 Seasonal Changes in the Composition of Particles Settling to the Hypolimnion

The above studies suggest that *P. hoyi* could obtain a substantial portion of its nutrition in spring before stratification. Phytoplankton dominance in Lake Michigan shifts from diatoms in the spring to cryptophytes and other small flagellates in the late summer (Figure 34.3; Fahnenstiel and Scavia 1987b). The large, heavy diatoms, i.e., the *Melosira* spp. that often are present in Lake Michigan during spring (Holland and Beeton, 1972; Fahnenstiel and Scavia, 1987b), may become directly available to *P. hoyi* either through turbulent mixing during isothermal periods, or by rapidly sinking through the water column.

Unfortunately, during spring when the lakes are not stratified, inputs of "new" organic particles from the epilimnion cannot be readily distinguished from those of resuspended organic particles, if comparisons are based only on carbon or AFDW analysis. The problem of quantifying spring inputs of "new" POC was circumvented by enumerating algae in Lugel's preserved sediment trap samples and converting the results to POC concentrations based on size measurement (Fahnenstiel and Scavia, 1987a). In a comprehensive study of the dynamics of phytoplankton at an offshore station (100 m depth) in Lake Michigan, both zooplankton grazing and particle settling rates were evaluated seasonally as processes for removing phytoplankton and other particles from the epilimnion (Figure 34.4; Scavia and Fahnenstiel, 1987). The algal loss rates due to sedimentation from the epilimnion decreases from 5–12 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ in early spring to $<0.5 \mu\text{g C l}^{-1} \text{ d}^{-1}$ during summer stratification (Figure 34.5). Algal losses in the spring were strongly dominated by diatoms that constituted $>95\%$ of the settling algae. Losses of settling phytoplankton were much smaller in the summer than in the spring, but diatoms still constituted from 23 to 62% of the total phytoplankton collected in the traps. Diatoms constituted only 5% of the total phytoplankton in the epilimnion during late summer, but settled out more than the other species (Scavia and Fahnenstiel, 1987). Epilimnetic zooplankton grazing on algae followed a seasonal pattern inversely related to that of algal settling into the sediment traps; grazing losses were lowest in the spring but increased as the season progressed (Scavia and Fahnenstiel, 1987).

The percentage of total POC accounted for by algae in the sediment-trap materials decreased from 16 to 95% in the spring to 0.4 to 2% during summer stratification. Thus, the quality as well as quantity of settling POC changed

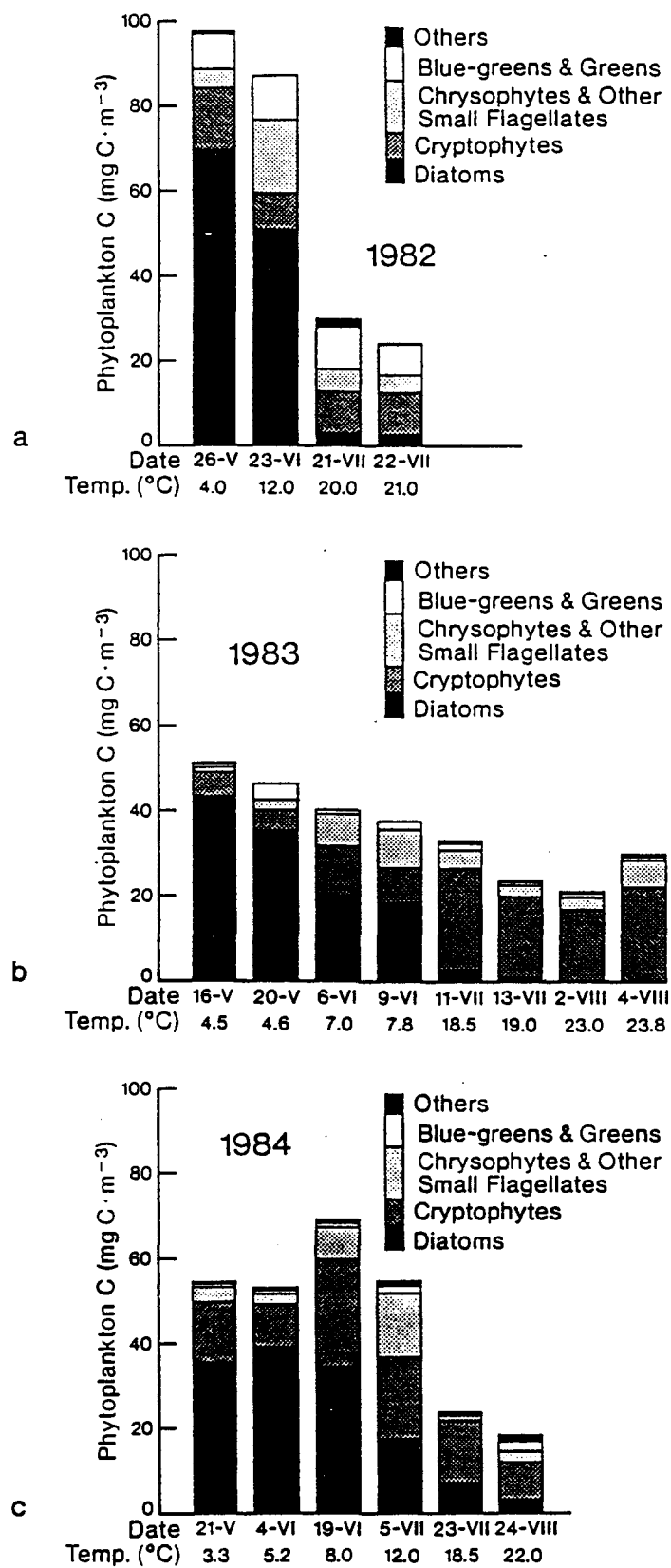


Figure 34.3 Phytoplankton composition in the epilimnion at various dates and temperatures in (a) 1982, (b) 1983, and (c) 1984. (From Fahnenstiel and Scavia, 1987b.)

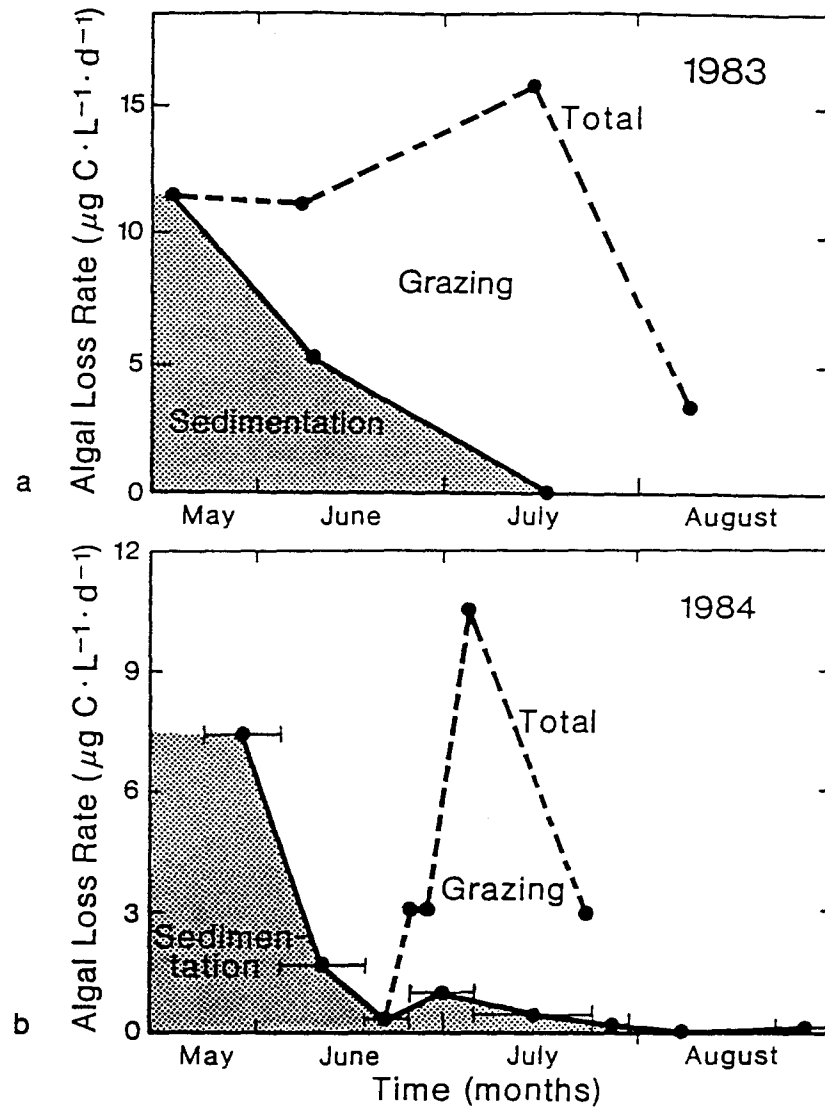


Figure 34.4 Partitioning of total loss rate (grazing plus sinking) during the field seasons of (a) 1983 and (b) 1984. (From Scavia and Fahnenstiel, 1987.)

substantially with season. During stratification, a substantial portion of the settling POC was detritus (e.g., zooplankton fecal pellets or residues of dead algal cells) rather than living phytoplankton. Feces from pelagic zooplankton and other detrital particles would be less nutritious than fresh phytoplankton because part of the labile nutrients would already be removed. The potential capacity of the diatom phytoplankton bloom to support *P. hoyi* production in Lake Michigan can be roughly estimated from the primary production and phytoplankton species-composition data of Fahnenstiel and Scavia (1987a; 1987b). Integration of *in situ* measurements of primary production over the euphotic zone of Lake Michigan indicated that primary production rates were in the range of 300 to 420 $\text{mg C m}^{-2} \text{d}^{-1}$ during the spring diatom bloom (May measurements; Fahnenstiel and Scavia, 1987a). If (1) the diatoms are assumed

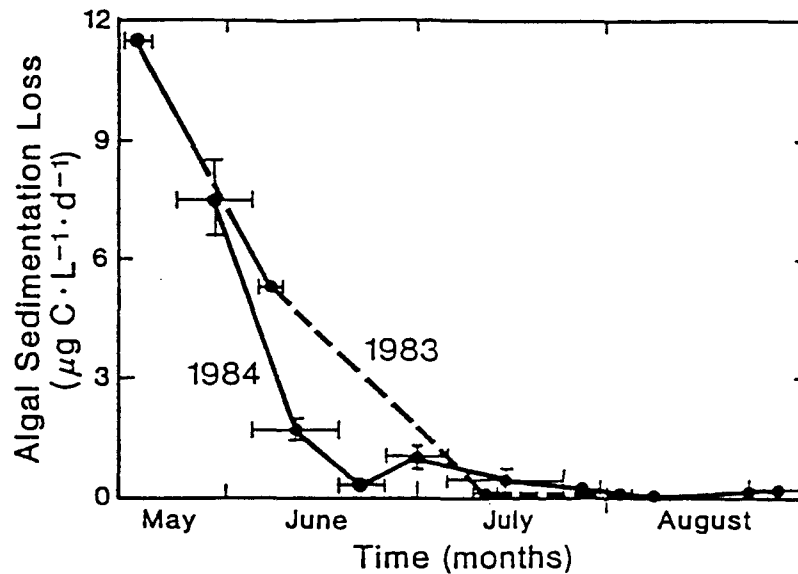


Figure 34.5 Sedimentation loss rates from algal counts of trap collections in 1983 and 1984. Horizontal bar lengths represent deployment duration; vertical bars are mean \pm standard errors, from multiple deployments in 1984. (From Scavia and Fahnenstiel, 1987.)

to constitute about 73% of spring phytoplankton (Fahnenstiel and Scavia, 1987b), (2) the duration of the bloom is about 60 days (Holland 1969), and (3) sedimentation is the dominant mechanism removing spring diatoms from the water column (Scavia and Fahnenstiel, 1987), then potential annual input of diatom carbon to the hypolimnion from the spring bloom would be 13 to 18 g C m⁻². This production would be adequate to support annual *P. hoyi* production (4.1 to 8.2 g organic C m⁻²) as calculated above. Recent calculations (Laird et al., 1988) suggest that the above estimate for diatom production may be too high because diatoms have slower growth rates than most of the other species of epilimnetic phytoplankton found in the spring bloom. However, even with this more conservative approach for estimating diatom production, spring diatom production would still supply as much as one-third of the energy required to support annual *P. hoyi* production.

All of the above calculations must, of course, be interpreted with caution because of the potential errors in extrapolating results from a relatively small number of field measurements, made in different investigations, to more general interpretations. Despite such precautions, they do suggest that the spring diatom bloom is an important source of food for *P. hoyi*.

34.3 Summary and Discussion

In agreement with previous productivity results on *Pontoporeia affinis* in the Baltic Sea, *P. hoyi* appears to have developed a feeding strategy that enables

it to thrive in low-nutrient, temperate aquatic systems such as the upper Laurentian Great Lakes, according to the following scenario (diagrammed in Figure 34.6): During spring holomixis when silica is available and temperature and light conditions are appropriate, large diatoms are abundant in these lakes. These diatoms are not grazed significantly by pelagic zooplankton because of their large size and fast sinking rates. In addition, concentrations of zooplankton are relatively low in the spring. The large size and high density of the spring diatoms cause them to settle out of the pelagic zone into the hypolimnion where they are directly (or indirectly) available to *P. hoyi*. This "seasonally available" energy is accumulated by *P. hoyi* in the spring as lipids, and, these lipids are used during the rest of the season when both the quantity and quality of incoming available food is low. As the summer stratification progresses, silica limitation causes the diatoms to decline and dominance to switch to other phytoplankton species (Schelske and Stoermer, 1971; Fahnenstiel and Scavia, 1987b) that tend to be grazed more efficiently by zooplankton. As a result, the composition of the dominant settling particles changes from diatoms to zooplankton feces and other detrital residues with low nutritive value.

The apparently direct transfer of nutrients/energy from large diatoms to *P. hoyi*, that is, in turn, eaten directly by fish, has interesting and important implications in comparative energy-transfer routes in Great Lakes food-web dynamics. The large size of spring diatoms compared to other phytoplankton, and of *P. hoyi* relative to most pelagic zooplankton, should make this energy-transfer route more efficient for fish production than would be true for traditional pelagic or microbial food webs. Only one intermediate trophic step may be required to convert photosynthetically fixed energy into a form (*P. hoyi*) sufficiently large to be readily eaten by fish. In contrast, energy originating from the microbial food web would usually require more trophic transfers with

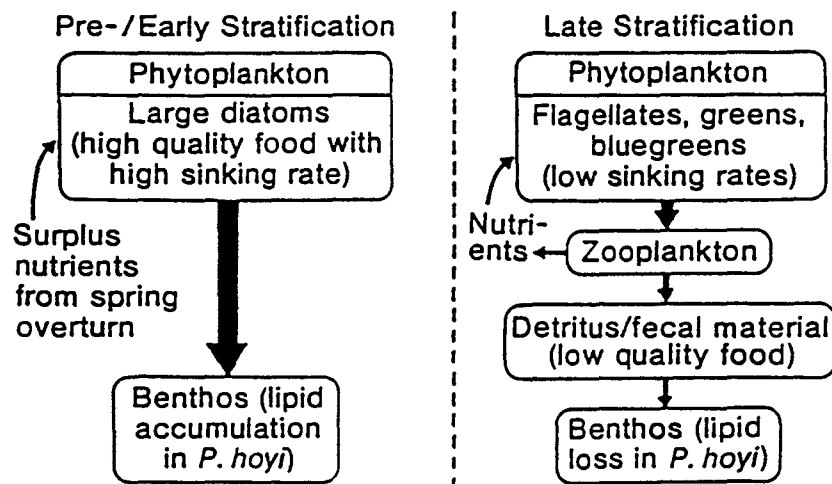


Figure 34.6 Schematic diagram of a conceptual model of the predominant processes for energy flow from phytoplankton to the benthos during (left) the pre/early stratification period (right) the late stratification periods, in southern Lake Michigan.

associated energy losses before a small portion of the energy can be incorporated into upper trophic levels (Ducklow et al., 1986). The classical food web, including intermediate-sized phytoplankton and zooplankton, falls between these two extremes. Another factor that appears to make *P. hoyi* an efficient food-web intermediate is its ability to accumulate high levels of lipids. Lipid energy is transferred more efficiently through the food web than is energy from other organic nutrients (Stewart et al., 1983).

The seasonal, direct transfer of biochemical energy from pelagic phytoplankton to benthic macroinvertebrates, which in turn serve as fish-prey, has not been studied extensively for a broad spectrum of lakes of different size and nutritional status. However, certain lake characteristics appear to be necessary for this phenomenon to be ecologically important:

1. Abundant oxygen and low temperature in hypolimnetic waters
2. Development of algal bloom(s) (e.g., a spring bloom of large diatoms) with high sedimentation loss rates and minimal euphotic grazing losses, and
3. A dominance of macroinvertebrate populations that can use seasonal nutrient inputs and are desirable prey for fish.

Low temperature is an important characteristic because animals with low metabolic rates (such as *P. hoyi*; Gauvin, et al., 1989) can survive with minimal "new" food inputs during much of the seasonal cycle and also because the rate of bacterial decomposition of settling materials is relatively low. Low-nutrient lake status is important because the hypolimnetic waters of eutrophic lakes tend to become anaerobic during stratification due to the oxygen demand of organic matter resulting from high primary production rates in the water column. Seasonal or episodic inputs of nutrients to the euphotic zone, such as occurs in temperate lakes during spring turnover, provide a means for phytoplankton blooms to occur in otherwise low-nutrient waters. As mentioned above, large diatoms such as *Melosira* in these blooms are not quantitatively grazed by pelagic zooplankton because of their size and relatively short residence times, relative to zooplankton regeneration times, in the pelagic zone. On the other hand, phytoplankton that do not readily settle to the sediments would be prone to ingestion or decomposition in the water column. Finally, conditions, like those mentioned above, must be appropriate for the development of high populations of macroinvertebrates, such as *P. hoyi*, *M. relictus*, or possibly Chironomids, that can effectively cope with infrequent inputs of high-quality food and provide a food base for fish. These conditions occur in several large, monomictic and dimictic lakes and some relatively small, oligotrophic lakes but would not apply to warm-water lakes or highly eutrophic ones.

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